Energy Transfer to Upper Trophic Levels on a Small Offshore Bank

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LONG-TERM GOALS

We propose to combine field observations and laboratory experiments to understand the coupling of physical and biological processes that transfer energy from lower to higher trophic levels on a small offshore bank. We focus this study on Platts Bank, in the western Gulf of Maine, and on the the relationship between internal waves, patchiness of planktonic organisms (especially euphausiids, *Meganyctiphanes norvegica*), and feeding and residence times of upper trophic level predators (marine and avian, but especially baleen whales, and particularly the humpback whale, *Megaptera novaeangliae*). Observations from Platts Bank and other feeding hotspots in the Gulf of Maine show that high levels of feeding activity are ephemeral—sometimes very active, often not. Differences can exist between weeks and between years. Our goals are to understand the factors that drive the "on" and "off" patterns of feeding at features such as Platts Bank, and to gain insights into the foraging strategies and mechanisms employed by highly mobile predators to exploit ephemeral and scattered feeding locations.

OBJECTIVES

1. Quantify patterns of upper trophic level use of Platts Bank over multiple years, extending observations from the original two years of observation (2005-06) that preceded this award.

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14. ABSTRACT

We propose to combine field observations and laboratory experiments to understand the coupling of physical and biological processes that transfer energy from lower to higher trophic levels on a small offshore bank. We focus this study on Platts Bank, in the western Gulf of Maine, and on the the relationship between internal waves, patchiness of planktonic organisms (especially euphausiids, Meganyctiphanes norvegica), and feeding and residence times of upper trophic level predators (marine and avian, but especially baleen whales, and particularly the humpback whale, Megaptera novaeangliae). Observations from Platts Bank and other feeding hotspots in the Gulf of Maine show that high levels of feeding activity are ephemeral?sometimes very active, often not. Differences can exist between weeks and between years. Our goals are to understand the factors that drive the ?on? and ?off? patterns of feeding at features such as Platts Bank, and to gain insights into the foraging strategies and mechanisms employed by highly mobile predators to exploit ephemeral and scattered feeding locations.

15. SUBJECT TERMS

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2. Describe behaviors adapted to feeding on Platts Bank and foraging on networks of scattered feeding sites such as Platts.

3. Measure and describe the internal wave field, associated velocities, and euphausiid distribution and abundance patterns.

4. Use field and laboratory studies to document and quantify the behavior of euphausiids and the coupled bio-physical processes that affect surface patch formation, in particular testing the hypothesis that internal waves help drive surface aggregations and upper trophic level feeding on Platts Bank.

5. Consider if and how the above mechanisms may apply to other regions of the Gulf of Maine, based on bathymetry, internal wave propagation patterns (e.g., from SAR imagery), historical and present-day information on whale feeding areas, and opportunistic sampling.

APPROACH

1. Use standard survey methodologies for enumerating large and mobile predators (marine and avian) on Platts Bank.

2. Develop a protocol for documenting predator orientation and behavior.

3. Use acoustic techniques (sound scattering) to survey the internal wave (IW) field and biological sound scattering on and around Platts Bank. In 2007 we continued use of a 75 kHz echosounder which worked well but was non-standard. In 2008-09 we used a Biosonics

4. Measure at multiple scales the properties of internal waves, including amplitudes, frequency, and water velocities that would affect planktonic organisms. CTDs and a thermistor chain (T-chain) precisely measure vertical displacements and frequencies of IWs. CTDs are deployed in cast and fixed-depth modes. The T-chain consists of 10 rapid-response (2 s, accurate to 0.01 °C) thermistors located every 2 m along a data cable (Precision Measurement Engineering, Carlsbad, CA). Depth of the bottom thermistor is ascertained with a VEMCO internally recording temperature and depth sensor. A 1200 kHz RDI ADCP measures water column velocities at 25 cm vertical resolution down to about 15-17 m, sufficient to study the region of most interest above the seasonal pycnocline and the propagating internal waves. A Nortek velocimeter (6 MHz, 3D velocity) measures velocities at 1 cm^3 scale at controlled depths. We have deployed the above using several methods to optimize data quality: (1) keeping the vessel at anchor; (2) drifting; and (3) tethered and untethered spars. Spars were designed to dampen movements from small surface (wind) waves and generally worked well in that regard, but substantially increased deployment and relocation times. They also prevented us from getting measurements close to the surface, so we did not use them in our final year.

5. Observe the behavior of euphausiids in the field with underwater video camera supplied with natural or IR light, attempting to do so in swarms and in the presence of internal waves.

6. Observe the behavior of euphausiids in a laboratory flume, using water velocities equal to those measured in the field.

7. Measure the mechanosensory/neurophysiological threshold for euphausiid response to fluid motion by placing microelectrodes into the antennules while the animal is exposed to well-controlled fluid signals created by the flume.

We received extremely valuable advice and assistance with our early acoustic work from Andone Lavery, Timothy Stanton and Peter Wiebe, all at the Woods Hole Oceanographic Institution. A. Lavery served on the MS Committee of a graduate student (Adam Baukus) in L. Incze's laboratory. An MS degree and thesis were completed and a paper in Marine Ecology Progress Series was published in 2008.

WORK COMPLETED

At sea: Only a small amount of sea time was funded for 2009. We used this to (1) improve on velocity meaurements of the near-surface flow of water during the passage of internal waves; (2) conduct a few spot-surveillances of Platts Bank for recording whale and other top-predator presence and feeding activity; and (3) investigating *in situ* the internal wave field at a historically active feeding area along the edge (80-100 m isobtah) of the Maine coastal shelf 58 nm north-northeast of Platts Bank. While all of these were valuable activities, our top priority was obtaining the near-surface measurements listed in (1) above. In previous years we recorded the spatial and temporal patterns of internal waves (IWs) and krill patches, and from these data the flow patterns and velocities can be approximated. However, our model of how krill patches form at the surface depends critically on the behavior and swimming speed of the krill relative to the horizontal and vertical velocities of the water. Specifically, we hypothesize, based on observations, that the horizontal displacements of water in the lee of an IW exceed the swimming speed of krill, but the subduction speeds do not. Horizontal velocities are large, and therefore reasonable uncertainties in estimating the speeds are not fatal. Vertical velocities are estimated from continuity arguments, the estimates are sensitive to assumtions about the width of the downwelling stream, and the predicted velocities are close to the estimated swimming speeds of krill. For that reason, direct measurements are essential to testing the hypothesis. We were successful in obtaining those measurements (see Results), using the same methods we developed in 2007 and 2008. Instruments were: a 1200 kHz ADCP, a 20 m chain of rapid-response thermistors at 2 m vertical spacing, fixed-depth and cast-mode CTDs, and a Nortek Velocimeter for point measurements (1 cm^3 volume) at 2m depth (see Approach for details). Nortek measurements were made at 64 Hz at a distance of 14 mm from the probe, which was oriented into the current by a vane attached to the sampling frame. To enhance detection in the relatively clear offshore waters, the water was seeded with MgCO3 dissolving from a small mesh bag suspended upstream of the probe.

In the Laboratory: Our emphasis this year was obtaining krill in good condition for neurophysiological measurements in the lab. Because krill cannot be obtained in reliably good condition with regular sampling nets, which must be towed at high speeds, we planned to capture them with dip nets from surface patches. This would have been easy in prior years, but these patches did not occur in 2008 during our field studies. Consequently, David Fields collected specimens of the same species near Bergen, Norway in June of this year (he was there on another project, and this had always been our "Plan B"). Krill were caught in light traps deployed overnight at 35 m depth. Typically, large numbers of juveniles and a few adults were caught. Measurements were made only on adults of similar size to those in our study area.

Individual krill were tethered in the center of an 8 liter vessel (Fig. 1). The test antennae were pierced at the articulation between the 2^{nd} and 3^{rd} segment of the biramus antennule (Fig 2). Voltage

differential within the appendage was measured using an insulated 5 MΩ tungsten probe (FHC) with a 1 μm exposed recording tip. Although we surveyed a variety of sites along the antennules, the distal region consistently produced the highest probability of recording clear action potentials and we subsequently confined our recordings to these sites. This area is near the antennal nerve containing axons from mechanosensory cells on the antennule, and allows us to record electrical signals from a variety of individual neurons.

The voltage signal was normalized to a silver reference wire mounted in the water bath and amplified 100× using a DC pre-amplifier and secondarily amplified up to an additional 10× using an APM analog-to-digital interface (FHC), and subsequently stored digitally using a Marantz PMD671. Signals were pre-filtered for 50/60 cycle noise using a HumBug (Questscientific Instruments). Data were analyzed off-line by inputting the recorded signals into signal processing software (Datawave) and the neural responses sorted based on their waveform characteristics (*e.g.*, peak and valley amplitude, rise time, offset slope) in order to identify individual neurons. We used this analysis to determine instantaneous spike frequency and the number of spikes occurring in response to each stimulus presentation. All responses were corrected for background activity. We are now analyzing the data for neural responses to forces that typify the surface ocean around Platts Bank.

RESULTS

Fluid velocities Vertical water velocities varied considerably with depth in the water column. In 2008 we measured fluid velocities at the midpoint of the internal wave centered on the thermocline (the location of maximum horizontal and vertical speeds). We reported on these last year. During 2009 we measured fluid velocities near the surface (1-3 m) where patches of krill have been found to accumulate. In this report we concentrate on the measurements made this year. A paper is in preparation in which we will combine results from the total field years we had with prior funding (2005) and this project (2006-2009).

Figure 3 shows a plot of the horizontal (3A) and vertical (3B) velocity near the surface (3 m depth) compared with the temperature fluctuations in the upper 20 m caused by the passing of several internal waves. What is immediately clear is that the strong temperature fluctuations in the pycnocline cannot fully predict the fluid dynamics in the upper water column where the temperature shows little to no variation (Fig. 3C). As a result, upward and downward flows in the divergent and convergent regions near the surface must be resolved with direct velocity measurements. These show that vertical velocities near the surface are on the order of +/-2 cm/s (upward and downward), and generally they range from 10-20 cm/s in the horizontal along the maximum flow axis. The mean positive flow of approximately 10 cm/s is caused by slippage between the boat and the tidal current, which varies over time as a function of location on the bank (accelerated currents due to shoaling topography), time in the tidal cycle (current speed), and slight variations in surface winds (which were light, but nonetheless affect the boat relative to transport in the current alone). To better assess the velocities associated just with IW passage, we recalculated the velocities based on a running mean every 10 minutes (Fig. 4).

Neurophysiology Velocity data used in our trials ranged from ~16 cm/s to 0 cm/s (Fig. 5). Data were recorded from 4 animals and 7 different neurons. Neural firing rates showed a clear dose response with respect to increasing vertical velocity. Fluid motion as low as 2 cm/s were easily detected by the krill. We are currently analyzing a few experiments with extremely low flow rates to find minimum threshold values for detection.

Behavior in a flume 2009 experiments have not been analyzed. We will do this wintr 2009-2010.

IMPACT/APPLICATIONS

We plan to increase knowledge of krill behavior in offshore waters, including vertical distribution, interannual variability in abundance, interactions with internal waves, and mechanisms of patch formation. In addition, we will define thresholds for reactions to flow fields that should have broader application than just internal waves or Platts Bank. By studying bio-physical mechanisms and upper trophic level behaviors on Platts Bank, we hope to provide insight into the processes that affect good and poor feeding conditions in areas of rapid topographic relief, such as Platts Bank, and the foraging behaviors and strategies that allow highly mobile, upper trophic level predators to exploit scattered and ephemeral feeding areas. This would help to explain vagrancy/residency patterns and movements of animals, including the large whales.

RELATED PROJECTS

This project has a relationship with the Gulf of Maine Area Program of the Census of Marine Life (http://www.usm.maine.edu/gulfofmaine-census/), which funded the first two years of observations on Platts Bank and led to the current research program funded by ONR. The Census is focused on defining patterns of biodiversity in the oceans and the processes that shape them. The Gulf of Maine program has the additional aim of describing how that diversity influences the ecosystem, and how diversity and functionality can be maintained. Incze is the lead PI on the program, and Kraus leads the upper trophic level expert group. The census is entering its synthesis period in 2009-2010.

PUBLICATIONS

Stevick, P., L. Incze, S. Kraus, S. Rosen, N. Wolff and A. Baukus. 2008. Trophic relationships and oceanography on a small offshore bank. Mar. Ecol.-Progr. Ser. 363: 15-28.

Baukus, A. 2008. Importance of internal waves for the density, distribution and trophic dynamics of euphausiids on a small offshore bank. MS Thesis, University of Southern Maine, Portland, ME. 58 p.

Publications in prep.

Incze, L.S., A. Baukus, D. Fields, N. Wolff, S. Kraus. Formation of krill (*Meganyctiphanes norvegica*) surfaces patches through interactions with internal waves. In prep. For Limnbol. Oceanogr., planned submission in February 2010.

Baukus, A., L.S. Incze, N. Wolff and S. Rosen. Relative strength of biological and physical sound scattering: Krill (*Meganyctiphanes norvegica*) and an internal wave field. In prep. For Ices J. Mar. Res., planned submission in March 2010.

Fig 1. Krill tethered from above and shown in relationship to the pipette (lower right). Yellow arrow shows location of the tungsten probe.

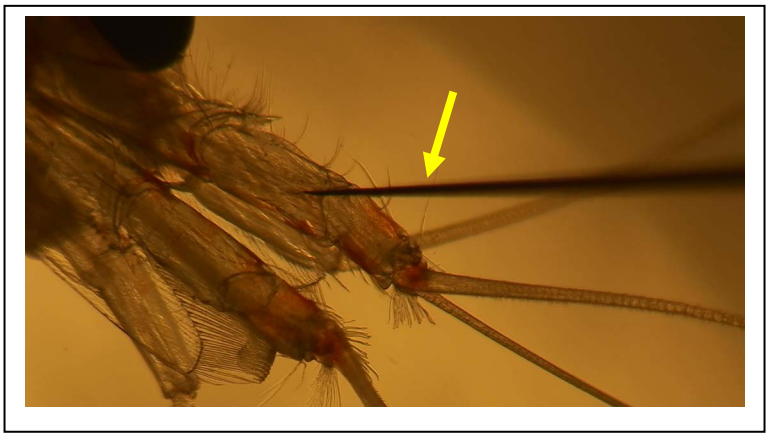

Fig. 2. Close up of the antennule of Meganyctiphanes norvegica showing the insertion of the tungsten probe (yellow arrow).

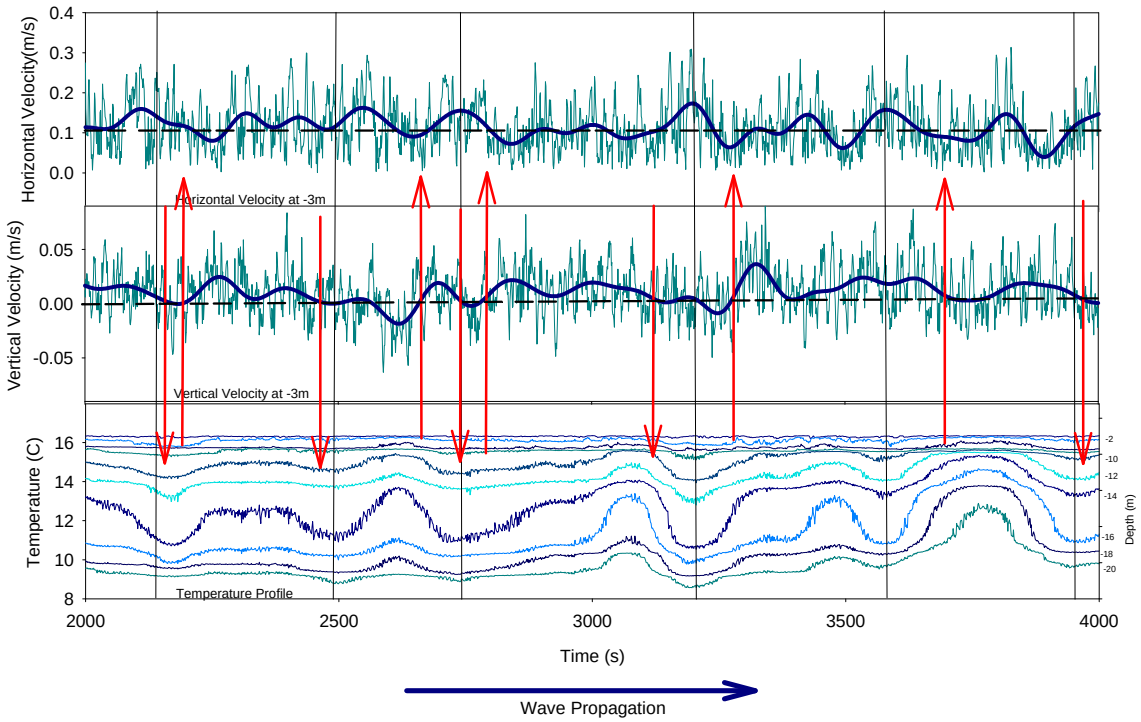

Figure 3. Small scale fluid velocity in the A) horizontal and B) vertical directions as measured by the Nortek Velocimeter at 3 m depth. C) Temperature shift due to passing internal waves measured with a 10-node rapid response thermister chain with nodes at 2m depth intervals from 2-20 m. The waves are traveling from left to right. <u>Rising temperatures</u> mark a <u>trough</u> in the thermocline (because warmer surface waters are found deeper in the water column). Red vertical arrows mark changes in flow from up-welling and down-welling based on direct velocity measurements, but the mean vertical is slightly positive. The positive horizontal mean velocity results from slippage between the vessel and the tidal current, which varies over time (see text). Velocities are adjusted in Figure 4.

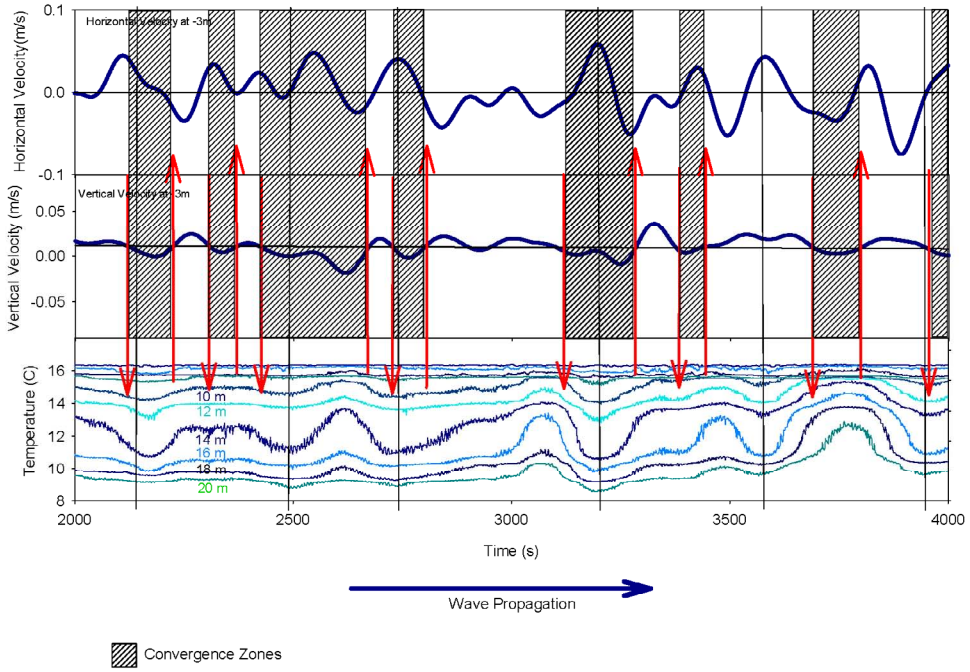

Fig. 4. Vertical and horizontal velocities at 3 m depth, associated with passage of internal waves over the top of Platts Bank, calculated using a moving 10 minute averaging period to eliminate variations in slippage between the drifting vessel and the water (cf. Fig. 3). There is a small net upwelling (~1 cm/s), which we attribute to the effect of tidal currents flowing over the crest of the bank. The lower panel shows the temperature (y-axis) of the rapid-response probes at fixed depths (depths are labeled next to each colored line). At a fixed depth, <u>decreasing</u> temperatures indicate the <u>approaching crest</u> of an IW as cold isotherms are displaced upward, and vice versa. Maximum temperature response is near the pycnocline in depths of 12-16 m. Isotherms nearest the surface show small excursions, and the patterns of temperature and flow fluctuations near the surface are generally complicated relative to the signals in the pycnocline. Periods of downwelling (0-2 cm/s) range from 30 to ~300s duration and follow the peak horizontal velocities, which in this series (66 minutes long) are on order 5 cm/s.

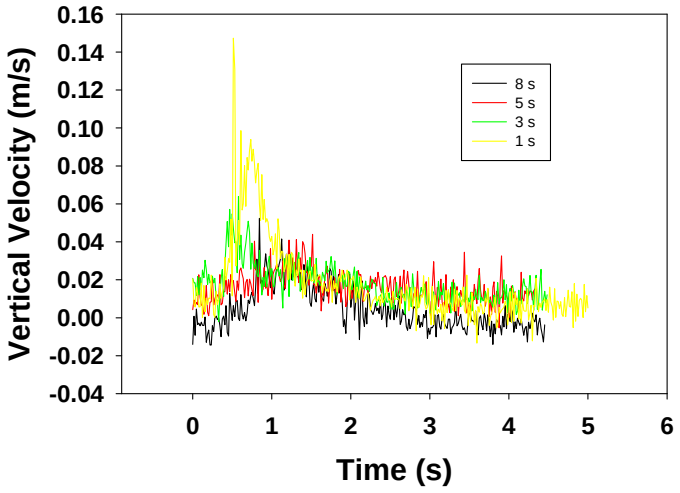

Figure 5. Vertical velocities generated in the laboratory by a constant-volume discharge released over different pulse-times using different pressures. The release duration is given in the legend, and the resulting velocities over time are shown in the main graph. These velocities were presented to a tethered Meganyctiphanes norvegica to measure neurophysiological response. The measurement is at the point of the probe insertion (Figs. 1 and 2). The nerve response results are shown in Figure 6.

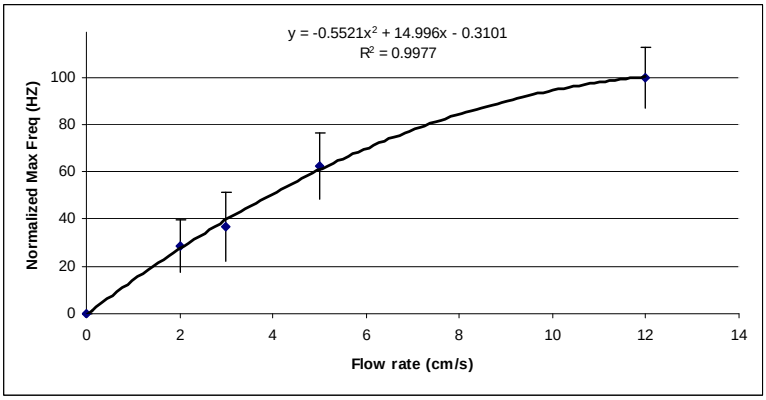

Figure 6. Dose response of M. norvegica neurons to fluid speed near the antennules (Figs. 1 and 2). Data show mean response (±1 SD) of all neurons (n = 7). Data were normalized to the maximum response of each individual neuron at a given flow velocity, which is the intensity relative to the maximal response observed (response measure ranges from 0 to 100%). Response intensity refers to the number of spikes over the 10 s stimulus period. There is significant (30%) response at 2 cm/s flow, and the neurons do not saturate until 12 cm/s.